

REPRODUCTIVE BEHAVIOR OF HAIRY WOODPECKERS II. NESTING AND HABITAT

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THE nesting period of Hairy Woodpeckers (*Dendrocopos villosus*) is of interest for a variety of reasons, one being that selective pressures are intensive at this time, and thus serve to bring out sexual differences in foraging, agonistic, and other behavior. Individuality appears to be well developed or at least observable in this species, as discussed in three previous reports. The first of these (Kilham, 1960) described a female which took the lead in an unusual courtship lasting through fall and winter months, and a second discussed sexual differences in feeding habits (Kilham, 1965). A third communication (Kilham, 1966a), reported observations on early breeding behavior, from pair formation in mid-winter to completion of nest excavations in early May, as well as a tabulation of the various vocalizations, drummings and other displays observable throughout the year. The present report, like the preceding one, is based on nearly twenty pairs of Hairy Woodpeckers observed in Tamworth and to a greater extent in Lyme, New Hampshire, from 1958 to 1966.

INCUBATION

Hairy Woodpeckers are subdued and silent while incubating eggs in the middle weeks of May and members of pairs usually make no more than a few intimate *teuk, teuk* notes when relieving each other at the nest. Pair H in Tamworth in 1958, however, was exceptional in the liveliness of its behavior. I was below the nest in an aspen on 19 May, when I heard *speaks*, then saw the two woodpeckers perched close together exchanging *joick, joick* notes before one flew off and the other entered the hole. Similar greetings accompanied all change-overs observed over the course of four days. Since the male, MH, spent the night on the nest, change-overs at the extremes of the day required a special timing. When I entered the woods before dawn on 20 May, for example, the first Yellow-bellied Sapsucker (*Sphyrapicus varius*) drummed at 4:45 AM and the first Yellow-shafted Flicker (*Colaptes auratus*) at 5:10, but there was no activity at the nest of the Hairy Woodpeckers until the female, FH, arrived with a medley of *joicks* to relieve her mate at 5:35 AM. It seemed probable that she needed half an hour to feed before settling down to her turn at incubating. Events took place in reverse in the evening, when MH came to relieve her at 7:30 PM which gave her about thirty minutes to feed before twilight. MH was late in arriving, however, on 20 May. FH was obviously nervous for she would emerge from the

nest, feed hastily on a nearby birch, then re-enter the nest only to emerge 5 minutes later for a similar performance. MH finally arrived for the night and took her place at 7:45 PM.

The members of Pair B in Lyme in 1965 contrasted with Pair H in having been exceedingly quiet during the incubation period. Incubation appeared to begin on 7 May when the drummings and vocalizations associated with the copulatory behavior of a few days before (for description of methods of communication, see Kilham, 1966*a*) tapered off rather abruptly. MB emerged from his nest hole at 6:30 AM as his mate arrived silently. He gave a Whinny, then flew to the far end of the wood and drummed a single burst before flying elsewhere. Throughout the next few weeks, I heard almost nothing from the pair, on visits paid nearly every morning. On entering the pasture woodland on 21 May, however, I realized almost immediately that the eggs had hatched by the behavior of MB who flew from his nest hole at 6:35 AM, did some quick, nervous preening on a nearby tree, then drummed at what for a Hairy Woodpecker was a very rapid rate of 16–20 bursts a minute. I had rarely heard him drum at a rate of over 5 bursts during the early breeding period from January through April. His behavior on 21 May was obviously unusual.

NESTLING STAGE

Table 1 presents uniformities of behavior observed among Hairy Woodpeckers during the nestling period. In retrospect, however, it was rather the diversity and adaptability of the species, not only between adjacent pairs but also within the same pair in successive years, which impressed one. These situations were well exemplified by Pairs A and B, which bred in adjacent territories in 1964 and 1965.

Pair B.—The members of Pair B were closely adapted to each other and to their territory, or so it appeared from their quiet behavior, prolonged courtship (Kilham, 1966*a*), and close cooperation in successful nesting during 2 successive breeding seasons. The situation where I observed the nesting activities in 1965 was optimal in a number of ways. It was located in an open woodland which did not attract Starlings (*Sturnus vulgaris*), which can be effective competitors for nest holes, and the nest cavity was four meters up in the rotten center of an aspen (*Populus tremuloides*) of which the living outer inch of wood provided protection against predators.

At 6:30 AM on 22 May, the day after hatching, FB alighted below the nest hole with food in her bill, then entered to remain on the nest after MB had wriggled out from the tight-fitting entrance, giving low conversational notes as he did so. This close brooding of the young continued for the next five days. FB alighted on the sixth day with a few *teuk* notes, but her

TABLE I
GENERAL DIFFERENCES IN NESTING BEHAVIOR OF MALE AS COMPARED
WITH FEMALE HAIRY WOODPECKERS

Type of Behavior	Male	Female
1. <i>Foraging</i>		
a. foraging areas	away from nest	close to nest
b. prey sought	mostly in trees	trees, brush, ground
c. location of prey	deep in wood	superficial; under bark, etc.
d. size of prey	larger; bill fails to close	smaller; bill closes
e. manner of hunting	deliberate; works one place	keeps moving; restless
f. number visits to young	relatively few	3 to 4 × as many as M
g. care of young	less concern	more attentive
2. <i>Guarding of Young</i>		
a. general surveillance	little	maintained during day
b. special danger	remains close to nest	less involved
c. night	roosts in nest	never
d. reaction to danger	calm	hyperexcitable
3. <i>Other</i>		
a. nest sanitation	does most of it	infrequent
b. plumage, end of nesting	good condition	frayed and soiled

mate was not there. She entered to feed, then emerged with a mass of feces in her bill and flew 100 m with peculiar short, rapid wing beats before discarding it. This was one of the relatively few occasions on which I observed performance of nest sanitation by a female of *D. villosus* (see Table 1). Both sexes exhibit the same type of flight when carrying feces.

A number of other patterns of behavior observed for Pair B were ones common to various pairs of Hairy Woodpeckers. On 28 May, for example, FB made 5 visits at close to 5-minute intervals between 6:15 and 6:40 AM carrying insects so small that they barely protruded from her bill. It was apparent from watching and listening that FB was foraging for prey on bark and other locations located not far from the nest and always within hearing distance of the steady *pee-urp, pee-urp, pee-urp* vocalizations of the young. These calls are doubtless a stimulus driving females to incessant activity. The attentiveness of the female in care of young at this and other nests was reflected in their plumages, which became increasingly sooty and disheveled as the season progressed while those of the males, which had come to nests less frequently, remained as well-preened and sharply black and white as in early spring.

Male B took life in a more leisurely fashion than his mate. On 2 June, for example, when she made four visits with small insects between 6:40 and

6:50 AM, he came only once, but with a grub so large that he could not close his bill. He was about to enter when FB alighted close by. She greeted him with *chewk, chewk* notes, then moved to his place and entered as he gave way and flew to a tree 30 feet away to wait until she emerged. On this and other occasions, it appeared as if females of *D. villosus* were often dominant in the particular situation of feeding the young. On 2 June MB returned to the nest after his mate had left, fed the nestlings, then flew off carrying a fecal mass in his bill.

Although MB was generally away from the vicinity of the nest more than FB, he remained close when there was any danger to put him on guard. On 6 June 1965, for example, I found him giving an uninterrupted series of loud *speaks* near the nest tree. By searching neighboring trees I discovered a gray squirrel (*Sciurus carolinensis*) resting on a level with the nest hole and seven m away. These squirrels are a threat to the nest cavities of larger woodpeckers. Within a few days after the young had flown from the nest of Pair B, for example, a squirrel had gnawed and largely destroyed the entrance.

MB appeared to do little and FB nearly all of the feeding of the young in the last few days of the nesting period. The volume of vocalizations made by the nestlings had become considerable by 10 June. Two days later the nest was silent. Thinking it empty, I knocked hard on the tree trunk below and thus precipitated an alarm vocalization which I had not heard before, a harsh *scree* as a well-feathered nestling looked out, then dropped back out of sight to become silent again. When a parent approached and pecked nervously on a tree on seeing me, the young began a clamor of begging notes. All of them had flown by the following morning.

The 1965 nest of Pair B was in an optimal location and the woodpeckers experienced no serious interference from nest-hole competitors. Their 1964 nest, however, presented a more complicated situation. Although it also was within the rotten center of a living tree, a butternut (*Juglans cinerea*), the tree was between two fields on an aerial highway of Starlings which came to rest on it many times a day. In the few moments of their stay, they often edged over toward the nest hole of Pair B with evident interest and curiosity. On 5 June when an especially inquisitive Starling approached the nest hole, MB faced it in threat display, with bill raised and wings outspread. Both birds held frozen positions momentarily. Then FB joined her mate and the advance of the two of them together frightened the Starling away. Other birds of similar size, such as Catbirds (*Dumetella carolinensis*) and Brown Thrashers (*Toxostoma rufum*) which occasionally perched even closer to the nest hole, aroused no reaction on the part of the woodpeckers. It thus appeared that the Starlings were their chief concern.

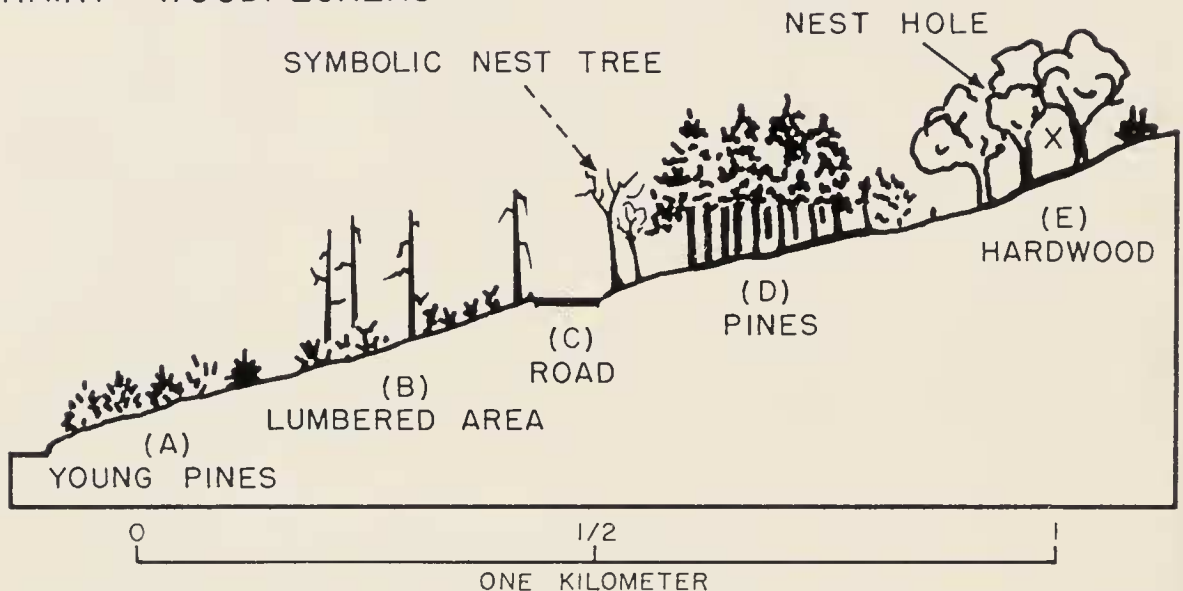
BREEDING TERRITORY OF A PAIR OF
HAIRY WOODPECKERS

FIG. 1. Diagrammatic cross section of breeding territory of Pair A, 1964. Activities noted for each part of the territory were: A. Cover of juveniles in weeks after nest-leaving. B. Early courtship in open area of drum trees and symbolic nest hole (see Kilham, 1966a). C. Section of territorial boundary; scene of conflicts between Male A and Male B in late winter. D. Foraging area of Female B, at distance from E, the location of nest hole.

The striking behavior of the woodpeckers in this year, 1964, as compared with 1965 was that one or the other of them was always on guard, presumably due to the Starlings. MB might fly in from the woods with food in his bill and FB leave as he arrived, but never before. He would go directly to the nest hole, feed the young, then ascend the same limb in a leisurely fashion, drumming here and there as he did so. His next move might be to drum a few loud bursts on a special resonating limb. While on guard duty for the next five or ten minutes he might shift idly from one neighboring tree to another, pick an insect from the bark, carry it to the nest, then pause for a rest below the entrance. As soon as FB returned, however, he would take off immediately. On some few occasions he would raise his bill and greet her with *chewki, chewki, chewki* notes before doing so. FB was by far the more active and restless of the two woodpeckers. She seldom either drummed or remained quietly in one place, but spent her time on guard duty hitching hurriedly over limbs and trunks of adjacent trees, even though insect prey became scarce on these over-worked locations. She occasionally flew to a dying elm 60 m from the nest, where her search for prey was more rewarding (Kilham, 1965). While on the elm she was still within full view of her nest.

In summary, one might say that (1) in the presence of a threat by Starlings,

the two woodpeckers cooperated closely in guarding their nest daily and at all times of day. (2) The same pair when nesting 250 m away in the following year and without any Starlings in the vicinity always left their nest unguarded while foraging for prey, except for the one special occasion when MB faced a gray squirrel. (3) As with other pairs of *D. villosus*, the greater activity and attentiveness of the female was generally apparent. (4) In spite of, or possibly because of, the differences of temperament of FB and MB, the two woodpeckers were never antagonistic but always appeared closely paired and devoted to each other, as had been the case throughout the early breeding seasons of two successive years (Kilham, 1966a). (5) MB was an unusually tame and leisurely individual. Neither parent, however, took much notice of me, even when I stood directly below their nest hole which was only six meters above the ground. Two of the offspring of Pair B which I kept under observation for several months in my aviary were quite tame. This tameness offered contrast to the rather different behavior of neighboring Pair A described below.

Pair A.—In 1964 this pair had an excellent nest hole, seven meters up in a living white birch (*Betula papyrifera*) in an open wood of red oak (*Quercus rubra*), birch, and hornbeam (*Ostrya virginiana*) (E in Fig. 1). The parent woodpeckers, however, seemed to find little prey in the area and took long flights away from their nest after feeding the young (for example to area B in Fig. 1).

MA was unusual in starting an almost uninterrupted series of vocalizations if I were within 20 or even more meters of the nest as he alternately approached, then circled away, making loud ruffle noises with his wings. His excitement was considerable. Aside from *speaks* given in a shrill fashion that made them resemble the *peek, peek* notes of a neighboring pair of Robins (*Turdus migratorius*) he gave sputters of his own variety. These had a quality of harsh laughter, of which a common sequence was *speak - chrr - charr - jer-jer-jer, charr - jer-jer*. FA was also excitable but less so than her mate. Her sputter was a more even *speak-ha-ha-ha-ha*. The young of this pair also seemed to be unusually excitable, and as they grew older they gave similar explosive sputters from within the nest. I had never heard such noises from the young of Pair B in two successive years. This hyperexcitability of MA, appeared to be one manifestation of a general eccentricity, evident not only in the prolonged courtship with FA (see Kilham, 1966a) but also by his rather extreme lack of aggressiveness whenever MB invaded his territory, a subject to be described in a subsequent report.

FA acquired a new mate, MA', in 1965. This new male had a calmer disposition, more similar to that of other males which I had observed. Pair A in both 1964 and 1965 showed a marked preference for seeking white birches

as nest trees. The 1964 tree was an excellent choice, since it was tall and vigorous with a nest entrance 7 m from the ground, made through living wood. If it could be considered at one end of the scale of suitability for nesting, the 1965 nest, located 3 m up in a rotten, fungus-grown birch stub, could be considered at the other, in regard to safety from predators. The stub stood in an open, lumbered area, where FA found insect prey without going beyond ear shot of the begging cries of her young (as I judged by the distance of 50 m at which I could still hear them). She was far more attentive than MA' in looking after the nestlings. On 3 June, for example, she brought small amounts of prey to the nest eleven times between 6:23 and 6:53 AM, at intervals of approximately two and one-half minutes, a rate far greater than that observed at any time for MA'.

In contrast to FA's mate of the year before MA' was a leisurely individual. He would stop to drum a few bursts, then take a long flight over the tree tops to some foraging area of his own. On many days he only made a sixth as many feeding visits as FA, but he nearly always brought in a large grub which protruded from his bill and after poking it into the bill of a young one, would help arrange the morsel in proper alignment for the nestling to swallow it.

Observations made on the feeding activities of FA in two successive years were, by chance, comparable for the middle of the nesting periods and can thus be summarized as follows. In 1964 with mate MA and poor foraging near the nest, FA made sixteen and MA, eleven, feeding visits to the young, in a total of two hours of observation time, while in 1965 with mate MA' and good foraging in the vicinity of the nest, she made twenty-three visits to the young as compared with only four by her mate. This amounted to 5.8 times as many feeding visits by the female as by the male.

The possibility that Pair A was nesting in a stub too rotten for safety was substantiated on 10 June. As I approached early in the morning I could tell by her vocalizations that FA was excited. She was still carrying insects in her bill as she moved excitedly two meters above a skunk (*Mephitis mephitis*) which was pushing its way through nearby vegetation. The skunk turned when I called to it, coming right to my foot with FA following closely and giving loud, repeated *chip - ha-ha-ha* notes as she did so. I now saw that the entrance to the nest in the rotten birch stub had been largely chewed away. The fledglings had survived, however, for one of them looked out through the ragged hole giving a series of vigorous sputters similar to those of its mother. I was also able to locate MA' in the distance by his steady succession of *speak*. Closer inspection of the nest stub revealed a few gray hairs caught on a rough place as well as a cluster of wide-spreading claw marks left on the birch bark below where a raccoon (*Procyon lotor*) had embraced the



FIG. 2. Direct view of Hairy Woodpecker defending nest hole showing disruptive color pattern. (Drawn by Cornelia Wood.)

stub. The proximity of the skunk at the time of my arrival had thus been a coincidence. It was remarkable that the raccoon had not been able to chew the nest out completely. My supposition was the MA', while roosting in and guarding the nest at night, had struck back at the raccoon in an effective manner, as illustrated by Figure 2, which is an imaginative reconstruction. This close encounter, if such took place, may have explained why MA' appeared to be particularly timid about approaching the nest on the early morning of 10 June. The two fledglings left their disrupted nest hole on 12 June when fully fledged.

Other aspects of nesting behavior.—Patterns of behavior common to Pairs A and B in two successive years as well as two other pairs observed during the nestling period in New Hampshire are summarized in Table 1. A few additional observations were as follows: (a) Nestlings could be quiescent at times, become vociferous as parents approached, then quiet down gradually after being fed. (b) Although adults entered the nest to feed smaller nestlings, they might rest on the outside and poke food to young, clinging within the entrance even sixteen days before nest-leaving. The open bills of parent and young met at angles to each other in the transfer of food. (c) After giving food, an adult might spend some moments poking back to aid a nestling arrange prey for swallowing. (d) If one Hairy Woodpecker arrived while its mate was still feeding young, there was often an exchange of *teuk*, *teuk* notes as the first bird flew away. (e) Although hand-raised nestlings occasionally formed fecal sacs, parents engaged in nest sanitation usually



FIG. 3. Vigorous feeding reaction of young Hairy Woodpecker, taking food from forceps at estimated thirteen days old.

appeared to be carrying irregular masses of fecal material. Whether sacs are formed or not, may be related to the type of diet at the time.

Pair G. 1966.—The nest of this pair was 7 m up in a dead beech (*Fagus grandifolia*) stub. The openness of the surrounding beechwood and its freedom from low vegetation enabled me to observe the flights of the parent birds to and from the nest to excellent advantage. What was striking under these circumstances was the amount of time spent by female FG on the ground. She appeared to be little disturbed by my presence 20 m from her nest and might alight as little as 10 m from me to forage. She tossed leaves aside in vigorous fashion, uncovered partially buried dead limbs of beech and other trees and sought prey from rotten wood, while moving rapidly and not pausing long in any one place. It would take her about five minutes on an average to find enough prey for a visit back to the nest. Her activities, however, might vary with climate and other conditions. The woodland floor, for example, had become relatively dry by mid-June but a heavy rain on the 16th made dead logs and branches soft and soggy. FG was especially active under these conditions, making as many as 7 visits to her nest in 23 minutes, all to and from an oak log which had been relatively hard in dry weather.

FG appeared to be much at home on the ground. She not only preened there in leisurely fashion on some occasions before foraging but, as I had observed on 6 May she even copulated there.

Very few other species of birds fed at the lower levels in the beech woods. Such birds as thrushes were all in mixed woods at the periphery of the wood leaving the female Hairy Woodpecker as seemingly the only one that could find prey efficiently on or near the ground under the beeches.

On 18 June after feeding the young from the outside MG paused to tap, then

drum-tap, just within the entrance. I had observed similar behavior for Male F in 1964. It seemed in both situations as though these drummings might be a way for the growing young to learn the displays of their species, or to have their innate proclivities for doing so reinforced.

I kept the captive young of Pair G in an aviary, the floor of which simulated the conditions of a woodland floor. Under these conditions the female, both as a juvenile and an adult spent much time foraging about on the ground. The young male, however, limited himself largely to a number of upright logs. Thus, a sexual difference observed in the field was duplicated to some extent in captivity. The significance of this difference of feeding habits may be in that female Hairy Woodpeckers have increased chances of finding food for their young, while remaining close to their nests.

OBSERVATIONS ON NESTLINGS

The principal observations on the nestling stage of Hairy Woodpeckers were made on two sets of young obtained in Maryland. In 1960 I studied three young from one nest which were of different sizes and stages of development. The feathers of the smallest were just emerging while the largest one had well-developed tracts of feathers. They had probably hatched on different days. The nestlings responded well to artificial feeding, making vigorous sucking motions on a small pair of forceps used to insert food into their throats (Fig. 3), and producing fecal sacs when probed after being fed. They were shut in a dark cabinet between feedings. Here they made low peepings which reminded me of a chorus of frogs in the swamp from which they had come. When I opened the cabinet door in the morning, all three heads shot out with necks outstretched begging for food.

The nestlings began to preen each other and to stretch their wings in a both-wings-up stretch at an estimated age of fourteen days. The gradation in size remained marked. At an average of eighteen days the largest was well-feathered and twice the size of the smallest, which was equally healthy and vigorous. The ivory white tip of the upper mandible (Fig. 4) as well as the fleshy knobs at the corners of the bill which aid parents in feeding their young, were still discernible at this age.

Several unplanned situations brought on vigorous defense reaction. On one of these, a fledgling Blue Jay (*Cyanocitta cristata*), caused the three young woodpeckers to crouch low, the fore parts of their bodies pressed down, and their heads elevated with bills wide open. In this position they made a harsh, pulsating noise, not unlike that of a young Starling. The reaction was brought on a second time when some new born suckling rats were placed in the same cabinet. It was a unique performance, for we saw nothing like it at other times.

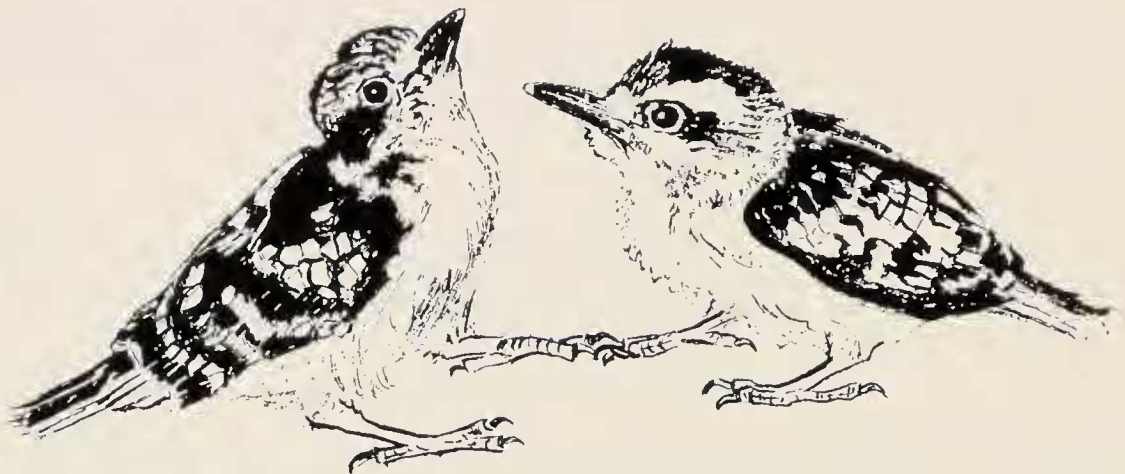


FIG. 4. Nestling at estimated eighteen days old still retaining white tip of upper mandible.

Another set of nestlings was obtained on 21 May 1957 when about half way through the nestling period or an estimated age of twelve days. Both were kept in a hollow log nest-cavity. They became upset if removed from it, as evidenced by efforts to climb upward and their settling down immediately when returned. The female was the larger of the two and she not only seized food in an aggressive manner but also pecked so hard at the smaller male, with fierce, persistent jabs, that he cowered as if in fright much of the time. On 24 May I put in a partition in an effort to ameliorate this situation. On 27 May, however, the female climbed over it to attack the male who did not defend himself on this or other occasions. Aggressiveness ceased at the time of nest-leaving, so completely that the two woodpeckers were able to rest together peacefully. Sielmann (1958) has described a situation closely similar to the above, in which he had to separate the smallest and weakest nestling in order to rescue it from attacks of the largest and fiercest of a brood of the Great Spotted Woodpecker (*Dendrocopos major*) which he raised in captivity from the time they were ten days old.

Time of Nest-Leaving Under Natural Conditions.—When I made my first visit to Nest B in Lyme at 6:15 AM on the day of nest leaving, 12 June 1964, two of the young had already flown and a last one was still chittering within the nest hole. I attempted to locate the fledglings which had left. One of them gave away his position by making *speak* notes in a small pine tree, close to the ground. While I was looking at him MB, who had been preening in a leisurely fashion close by the nest tree, came within 3 m, making *jeek* notes to the young one, and seemed unconcerned by my proximity. His mate, on the other hand, was full of activity as she hitched up a dying elm, prying out larvae from the bark and feeding them to a second fledgling who was following her up the trunk, jerking his body, half-starting his wings, and making a sputtery whinny as he did so.

FB flew back to the nest hole some minutes later with prey in her bill. The third and last fledgling, however, had already flown. FB bowed in and out of the entrance as if aware that another young one was to be accounted for, but uncertain where it might be. She flew about the nest tree for several minutes, swinging her head to look about and giving excited Speaks. She then flew to the trunk of a neighboring tree as the lost fledgling started upward from the ferns at its base, possibly in response to her vocalizations.

I interrupted these events by capturing two of the fledglings for further observations in the aviary. Under usual circumstances Hairy Woodpeckers cease to share the job of feeding their young after nest-leaving and are followed about in succeeding weeks by a particular offspring which is cared for entirely by one parent. I had thus created something of an experiment. With only a single young one remaining, which parent would care for it? There was actually little question, however, as I observed on the following morning when FB, who had been the more attentive in caring for the nestlings, was taking full care of the surviving juvenile. The latter made Speaks, Whinnies, and a *quare*, tree-frog like note, when she came to feed it. This was in a wood 200 m from the old nest. Vocalizations were even more lively on the following day when I came to the thicket of young pines. FB on this occasion flew to where her juvenile was lurking with a loud ruffle of wings, then burst into a series of exuberant *joick*, *joick* notes such as she had used earlier in the year in greeting her mate (Kilham, 1966a).

Comments on agonistic Behavior of Nestlings.—The harsh noises made by the nestling Hairy Woodpeckers on sudden threat were startling performances and comparable in this respect to the hissing vocalizations of nestling flickers, even though not snake-like. On 29 June 1957, I put an arm down into a flicker's nest. The nest was dark and silent beforehand, and the sudden, explosive, snake-like hisses of the young flickers, which were an estimated twelve to fourteen days old, were both unanticipated and frightening. According to Sherman (1910) flickers make hissing vocalizations steadily from the time they are a day old. She does not, however, describe the startling effects of sudden hissing as being a probable defense reaction. Sibley (1955) has described this type of behavioral mimicry for titmice (Paridae) and other birds.

Sherman (1910) noted in her observations of nestling flickers that some broods were more "quarrelsome" than others, a situation which may also be true for *D. villosus*, since the set of nestlings which I raised in 1960 were peaceful in contrast to the brood of 1957. A number of factors may be operative in determining the extent of agonistic behavior among nestling woodpeckers. One is that the nestlings hatch on different days so that some

are more developed and larger than others. The relative weakness of a small sibling may serve to initiate aggressiveness of older nestlings, which in turn may serve a biological function in survival if we consider the ways in which the attacks may take place under natural circumstances. Thus Sherman (1910), speaking of nestling flickers as fighting like "little demons at times," states that "Their battle-ground is in the vicinity of the hole. The one in possession of the hole maintains his supremacy there by occasional withdrawals of his head from the hole in order to deliver vigorous blows on the heads of all within his reach, causing them to shrink downward. This is the case with the stronger ones, the weaker ones frequently are driven from the vantage place." One can imagine that in adverse circumstances, such as poor foraging conditions in unseasonable weather, there could be survival value for the species in reducing the number of nestlings. The combination of varied ages of nestlings and fierce aggressiveness of the first to hatch, would thus provide mechanism for adaptiveness to environment, operative not only in regard to food supply, but also to space within the nest hole, if such were limited. This latter point can be a problem of consequence. If woodlands where woodpeckers nest have few suitable nest trees, the birds may be forced to excavate holes in nest trees that are below optimum in size. Not all of the young hatched could possibly reach the full size of fledglings under such circumstances. Hence survival of only two out of four, for example, would insure adequate space for the smaller number. This relation of brood size to adequacy of the nest tree is worthy of continued study. The situation first became apparent to me among Casqued Hornbills (*Bycanistes subcylindricus*) (Kilham, 1956), large hole-nesting birds which always lay two eggs, three or four days apart. Only one of the hatchlings, however, survives. The size of the bird combined with the general destruction of forests in Africa has made it very difficult for this species to find nest holes adequate in size.

While raptors such as eagles are not troubled by living space, they furnish parallels to woodpeckers and hornbills in several respects. As stated by Brown (1955) "eagles lay their eggs several days apart, and since they begin to incubate the first egg at once, the first eaglet hatches several days earlier than the second. As soon as this first eaglet is sufficiently active it starts to attack the other weaker eaglet with a viciousness which is hardly paralleled in the bird world." Brown is unable to explain this situation, in which "one eaglet generally kills the other."

NEST-HOLE COMPETITORS

While most pairs of Hairy Woodpeckers were little disturbed by my standing within 20 m of their nest trees in making observations, a few pairs were

more difficult of approach. As shown in examples below, this disturbed behavior appeared to be less a matter of chance variation than of stress carrying over from earlier competition with Starlings.

Pair Y, 1966.—This pair nested on a farm on the outskirts of Lyme and, as seemed inevitable, were dispossessed by Starlings from two successive holes excavated in exposed situations. By 10 May Pair Y was working on its third and successful nest hole. This was located on the under side of an arching limb of a butternut (*Juglans cinerea*), with an entrance pointing toward the ground and partially concealed by leafy branches, a type of location unattractive to Starlings in my experience. Both the male and female of Pair Y were highly excited and difficult to observe. During the incubation period, for example, Male Y made many *speak* notes, pecked on bark, or hastily preened in a quick, nervous, ineffective manner as he moved about the nest tree in the course of frequent change-overs at the nest. Neither he nor his mate were able to remain on the nest for very long. If he came to the entrance, he would bow in and out repeatedly, before swinging inside. His mate, FY, exhibited a similar type of nervousness throughout the nesting period. What was surprising, however, was that in Male Y this nervousness appeared to cease by the time the eggs had hatched, as was shown by his behavior on 5 June. On this occasion two juvenile red squirrels (*Tamiasciurus hudsonicus*) had begun to leave their nest in a limb above the one occupied by the Hairy Woodpeckers and were crawling about the nest tree. FY, when alone, was too excited to take effective action. She would pop into her nest hole, come out, fly to a neighboring tree, return, jerking her body about in exaggerated swings with head feathers bristling and while making almost incessant *chip* notes. Male Y, in contrast, flew quietly to the nest tree at 6 P.M. He alighted to one side of the nest, surveyed the two squirrels within only a few feet of where he clung motionless. Then he entered the hole and rested immediately with bill out, as if on guard. As with other pairs of Hairy Woodpeckers observed, this male appeared to have a temperament different from that of the female and one that made him a more effective guardian of the nest in the face of disturbing circumstances.

Pair E, 1965 and 1966.—The territory of this pair remained the same in two successive years. It consisted of a wooded slope of oaks and beeches terminating in an open beaver swamp, providing favorable habitats for flying squirrels and for Starlings respectively.* In 1965 Pair E had a first nest-hole eight m up in the straight bole of a beech tree. Female E entered the hole on 2 May and remained quietly inside as if incubating. On subsequent visits,

* There are two species of flying squirrels in central New Hampshire (*Glaucomys sabrinus* and *G. volans*) which are much alike in size and color and I made no attempt to differentiate between them under field conditions.

however, I found that the members of Pair E had abandoned this completed excavation, and had made a second one in another beech farther along the same slope. I watched them here without difficulty in June as they carried on nesting activities in quiet fashion. Their young left the nest successfully on 19 June. Subsequent observations indicated that the first nest cavity had been taken over by flying squirrels.

Starlings were the nest-hole competitors of Pair E in 1966. On 10 April, I found the two woodpeckers working on two excavations simultaneously, one in the straight bole of a beech tree, such as flying squirrels had taken over the year before and a second one in a dead elm, standing in the open swamp. Only the latter excavation was completed. I observed copulations of the pair near this cavity on 22 April, but Starlings, of which there were many about the chain of open beaver swamps below, had taken over from the woodpeckers by the end of the month. The woodpeckers returned to the wooded slope and nested in a tall white birch. I found that they had now become timid and excitable to an extent that I could only see them coming to the nest by approaching with care, then hiding at some distance. The behavior of the two birds thus exhibited a change, not only from what it had been earlier in the same spring, but also from that of the nesting period of the year before and one which persisted until the day of nest leaving.

Flying squirrels may slip into a nest hole when it is momentarily unguarded, thus presenting the woodpeckers with a *fait accompli* on their return. There is probably little they can do about it. When Starlings take over a woodpecker's excavation at the moment of its completion, however, it is by a hard, relentless struggle in which the teamwork and aggressiveness of the intruders always wins, or so it would seem from earlier (Kilham, 1960) and present observations, as well as those of Howard (1920), Löhrl (1957), and Shelley (1933) among others. Stickel (1963) has described a rather surprising lack of interest taken by a pair of Hairy Woodpeckers in a flying squirrel occupying the same nest tree.

DISCUSSION

Tinbergen's remark that "only a few workers recognize the amazingly high degree of adaptiveness to be found in numerous behavioural characteristics" (1955) is particularly pertinent to the present studies. The fact that the members of a pair of Hairy Woodpeckers are beautifully adjusted to each other, in most cases, as well as to the woodlands in which they nest is due in large measure, it would seem, to their preceding period of courtship (Kilham, 1966a). There are various expressions of this adaptiveness. Among these, one of particular interest to this observer is the separation of nesting duties between the male and female and the question of why these

duties should come to be divided in the way they are. Why is the male, for example, the one to spend the night on the nest, whereas the reverse is true among most species of passerine birds? Answers to these and other problems are sought below on a basis of observations made not only on woodpeckers but also on other species of unrelated hole-nesters including the Red- and the White-breasted nuthatches (*Sitta canadensis*) and (*S. carolinensis*) and Casqued Hornbills (Kilham, 1956).

An explanation of the male spending the night in the nest may lie in the fact that the nest-holes of such species as Hairy Woodpeckers are defensible fortresses under usual circumstances, as can be imagined by viewing a male resting inside, facing a predator (see Fig. 2). Its bill in this position becomes an effective weapon, as I have tested with individuals defending their roost hole in an aviary. Hairy Woodpeckers strike fast, hard blows and these should be enough to fend off a raccoon, especially when nest holes are built through living wood as they usually are. That a male may be able to protect its nest under even less favorable conditions is suggested by the account given of Male A' in 1965. Here a raccoon had been unable to reach the nestlings even though it had greatly enlarged the nest entrance built in rotten wood. A point to be made in these considerations, is that the defending woodpecker has to be aggressive to hold its position. The question then is which member of a pair of woodpeckers would be most likely to exhibit these qualities and strike back at a raccoon if necessary?

Field observations suggest that male Hairy Woodpeckers are not only the more aggressive, as is also true of many species of passerine birds in the breeding season, but also have the temperament needed in the presence of danger. This was well shown by Male Y, for example, when facing red squirrels within a few feet in 1966. Since female Hairy Woodpeckers have appeared to be overly excited and ineffective under such conditions, one may wonder whether males among woodpeckers have not come to replace them on the duty of night-on-the-nest, because of a premium put on their natural aggressiveness in terms of survival of the species. The bill as a weapon within a fortress has thus come to be associated with a behavior pattern making it effective. This is a situation which Waddington (1956) summarizes well in his analogy of the target-following gun.

The distribution of duties among the members of pairs of nuthatches differs markedly from that among woodpeckers, for here it is the females which not only spend nights on nests but also stay there during the day while incubating their eggs alone. The task of the males becomes limited to bringing food to the entrance to feed their mates at least in the earlier stages of nesting. In these connections, one might note that nuthatches do not have defensible nest-holes. Red-breasted Nuthatches usually nest in rotten stubs

where their small size and slender bills would offer unlikely protection against a raccoon, which could chew the nest open with little difficulty. White-breasted Nuthatches, on the other hand, have stronger bills and do nest in natural cavities within living trees, which might be likewise considered as natural fortresses. Their preference, however, is for cavities with large entrance holes. It would seem improbable that a nuthatch only partly filling such a hole with its body could fend off as common a predator as the raccoon, which could easily reach in behind it. Nuthatches actually have other ways of protecting their nests without reliance on meeting intruders head on. Their various methods of nest hole defense, including bill-sweeping, are reported elsewhere (Kilham, 1968).

According to Haartman's classification (1957) nuthatches are secondary hole-nesters, since they have spotted eggs and have probably acquired hole-nesting habits more recently than species such as woodpeckers which lay white eggs. Could it be that given more time, nuthatches might also evolve the habit of having males replace females on their nests at night? There would appear to be little indication of evolution in this direction at the present time. It is here that the habits of hornbills appear curiously parallel to those of nuthatches. Hornbills are primary hole-nesters, laying white eggs like those of woodpeckers but the females do all the incubating and rearing of the young, with the male having only a single duty of feeding his mate at the entrance (Kilham, 1956). The female hornbill is within a fortified nest and she has a powerful bill to defend it. This way of breeding depends on the female having a maximum of protection by laying eggs and incubating them without ever leaving the nest. The curious thing is that these habits are not altogether dissimilar from those of present-day nuthatches. The European Nuthatch (*S. europaea*), for example, even walls in its nest entrance, (see Löhrl, 1958) and is the only bird to do so outside of the group of hornbills, as far as I can determine.

The color patterns of the heads of Hairy Woodpeckers are strikingly disruptive if one is facing a roosting or nesting individual with its head drawn-back, ready to strike, from within a darkened entrance. This effect is only partly shown in Figure 2. In dimmer light, the black and white lines radiating from the base of the bill give the appearance of some snake-like creature, especially since the true eyes are concealed in black bands while the front portions of the white bands above them stand out as prominent false ones. This effect is increased when feathers on the top of the head are raised, as they may be in excitement. The sudden enlarging, or changing in shape of the two visible white patches gives an effect not dissimilar to the false eyes revealed on the unfolding of wing spots among certain moths.

Color patterns of hole-nesting birds may have adaptive significance and

this may be especially true of black patches concealing eyes. These patches are found in a variety of hole-nesters such as Red-breasted Nuthatches and Chickadees (*Parus atricapillus*) which resemble Hairy Woodpeckers in having nest entrances which exactly fit their head and body size. The black is absent, however, where head and entrance size are disproportionate. White-breasted Nuthatches and Tufted Titmice (*Parus bicolor*) which are without such patches, for example, nest in natural cavities with large irregular entrances. European woodpeckers of the genus *Dendrocopos*, however, present an exception difficult to explain. It would be of considerable interest to know if the species of woodpecker involved are exposed to different types of selection pressures or nest in a different fashion than their American counterparts. Photographs assembled by Blume (1963) help to visualize the appearance and nesting activities of Great Spotted Woodpeckers, which are similar to those described for Hairy Woodpeckers in many respects. The white patches around the eyes, however, are strikingly different.

Nest sanitation is another task performed by males among Hairy as well as Black-backed Woodpeckers (*Picoides arcticus*) (Kilham, 1966b) which are two species I have studied at the same time and in a similar manner. One can only hypothesize as to why females of the two species should take a much lesser interest in the performance, when they are in general the more active partner in the care of the young. A nest hole, however, is also a male's roosting hole. He is thus, in a sense, more the true proprietor and hence may be more concerned in keeping it free of fecal contamination.

The almost feverish activity of female Hairy Woodpeckers in foraging for their young, their hyperexcitability, and the soiled, frayed appearance of their plumages as the nesting season progresses, all suggest that the vocalizations of their young are constantly impelling them on their round of duties. Their mates on the other hand, spend much of their time beyond the range of these noises and this may account, in part, for their more leisurely demeanor. Some situations, however, tend to obscure the fact that females are the more attentive of the two partners in care of the young. One of these is the nature of the woodland habitat. If this is unfavorable for local foraging as illustrated in Figure 1, the female may have to travel farther away, beyond earshot of the young, and will visit her nest less often in consequence. A second situation concerns an observer standing too close to a nest hole so that only the male may continue to feed the young while his mate, being the more timid, stays away, a situation which I have also observed for Black-backed Woodpeckers (Kilham, 1966b) and which Steinfatt (1937) has described for the Great Spotted Woodpecker.

It is difficult to understand the *Umwelt* of Hairy or other species of woodpecker in any degree of completeness, "The *Umwelt* of any animal" being

“only a section carved out of the environment” (von Uexküll, 1957). Figure 1 is an attempt at such a section for a single pair. It shows that different parts of the territory were used by the Hairy Woodpeckers for different purposes over a long breeding period which began when the bare woods was filled with snow in mid-winter and ended when juveniles left their parents in mid-summer. Each phase of a breeding season interrelates with others. In many ways the period of actual nesting is the one of most interest, since it is here that selective pressures exerted by the environment are most acute.

SUMMARY

Observations on Hairy Woodpeckers indicate that males forage away from nests, making fewer feeding visits but with larger prey, whereas females forage within earshot of their young, making frequent visits as well as maintaining general surveillance. Variations in local ecological conditions may upset patterns of nesting behavior. Among varying factors observed were the suitability of the nest tree in terms of security from predation, the closeness of foraging areas, and the presence or absence of such nest-hole competitors as flying squirrels or Starlings. Hairy Woodpeckers are able to adapt to a wide range of conditions. Sexual differences in feeding and agonistic behavior as well as the closeness of pair bonds may account, in part, for this adaptability.

LITERATURE CITED

- BLUME, D.
1963 Die Buntspechte. A. Ziemsen Verlag. Wittenberg Lutherstadt.
- BROWN, L.
1955 Eagles. Michael Joseph, London.
- HAARTMAN, L. VON
1957 Adaptations in hole-nesting birds. *Evolution*, 11:339-348.
- HOWARD, H. E.
1920 Territory in bird life. John Murray, London.
- KILHAM, L.
1956 Breeding and other habits of Casqued Hornbills (*Bycanistes subcylindricus*). *Smithsonian Misc. Coll.*, 131.
1958 Pair formation, mutual tapping and nest hole selection of Red-bellied Woodpeckers, *Auk*, 75:318-329.
1960 Courtship and territorial behavior of Hairy Woodpeckers. *Auk*, 77:259-270.
1965 Differences in feeding behavior of male and female Hairy Woodpeckers. *Wilson Bull.*, 77:134-145.
1966a Reproductive behavior of Hairy Woodpeckers. I. Pair formation and courtship. *Wilson Bull.*, 78:251-265.
1966b Nesting activities of Black-backed Woodpeckers. *Couder*, 68:308-310.
1968 Reproductive behavior of White-breasted Nuthatches. I. Distraction display, bill-sweeping, and nest-hole defense. *Auk*, 85:477-492.
- LÖHRL, H.
1958 Das Verhalten des Kleibers (*Sitta europaea caesia* Wolf). *Zeitschr. Tierpsychol.*, 15:191-252.
- SHELLEY, L. O.
1933 Some notes on the Hairy Woodpecker. *Bird-Banding*, 4:204-205.

- SHERMAN, A. R.
1910 At the sign of the Northern Flicker. *Wilson Bull.*, 22:135-171.
- SIBLEY, C. G.
1955 Behavioral mimicry in the titmice (Paridae) and certain other birds. *Wilson Bull.*, 67:128-132.
- SIELMANN, H.
1958 Das Jahr mit den Spechten. Verlag Ulstein, Berlin.
- STEINFATT, O.
1937 Aus dem Leben des Grossbuntspechtes. *Beitr. Fortpflanzungsbiol. der Vogel*, 13:101-113.
- STICKEL, D. W.
1963 Interspecific relations among Red-bellied and Hairy woodpeckers and a flying squirrel. *Wilson Bull.*, 75:203-204.
- TINBERGEN, N.
1955 The study of instinct. Clarendon Press, Oxford.
- UEXKÜLL, J. VON
1957 A stroll through the worlds of animals and men. *Instinctive Behavior*, C. H. Schiller (ed.), Internat'l Universities Press, Inc., N.Y., 5-80.
- WADDINGTON, C. H.
1962 The nature of life. Atheneum, N.Y.

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